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A comparison of morphology and web geometry between hypogean and epigean species of *Metellina* orb spiders (family Tetragnathidae)

Thomas Hesselberg[1,2], Daniel Simonsen[1]

1 *Department of Zoology, University of Oxford, Oxford, South Parks Road, OX1 3PS, UK* **2** *Department of Biology, University of the Balearic Islands, 07071 Palma de Mallorca, Spain*

Corresponding author: *Thomas Hesselberg* (thomas.hesselberg@zoo.ox.ac.uk)

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Abstract

Studies on the behaviour of subterranean animals are rare, mainly due to the problems with collecting data in these inaccessible habitats. Web-building cave spiders, however, leave a semi-permanent record of their foraging behaviour, which can relatively easily be recorded. In this study, we compare size, leg lengths and web characteristics between hypogean populations of *Metellina merianae* with its close wood-inhabiting relative *M. mengei*. We confirm previous observations that *M. merianae* does not show any obvious morphological and behavioural adaptions to a subterranean life-style, although individuals of the cave species were significantly larger and had webs with relatively fewer radii and capture spiral turns than *M. mengei*. We were, however, not able to determine if these findings indicate a transition towards behavioural adaptation to caves or if they are a result of behavioural flexibility in response to the different humidity and temperature between caves and woodland. Finally, we did not find any effect of cave characteristics on either the number of radii or the area of the *M. merianae* web.

Keywords

behavioural adaptations, orb webs, morphological adaptations, troglophile, leg length, *Metellina merianae*, *Metellina mengei*

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Introduction

The unique adaptations to the dark and nutrient poor subterranean habitat have fascinated biologists since the dawn of speleobiology more than 200 years ago. Studies have discovered numerous examples of convergent evolution including physiological adaptations such as low metabolic rates and other mechanisms to survive long-term starvation (Hervant et al. 1997; Lipovsek et al. 2018), and morphological adaptations such as elongation of limbs, loss of eyes and pigments (Poulson and White 1969; Christiansen 2004; Culver and Pipan 2009; Mammola 2018). However, very few studies have looked into behavioural adaptations to the hypogean environment (but see: Juberthie-Jupeau 1988; Hoch and Howarth 1993; Parzefall 2005), likely because in-situ studies of animal behaviour are fraught with difficulties given the scarcity and inaccessibility of most cave organisms. Arachnids are promising candidate organisms for addressing this imbalance as they are one of the most numerous taxa in subterranean habitats, and display a wide range of interesting behaviours (Foelix 2011; Chapin and Hebets 2016; Mammola and Isaia 2017). Surprisingly given the lack of light and low abundance of flying insects, even orb spiders, whose two-dimensional webs are especially adapted to intercept and retain flying prey, are represented in the entrance and twilight zone of caves and mines with at least four genera in the family Tetragnathidae (*Meta*, *Metellina*, *Okileucauge* and *Orsinome*)(Eberhard 1990; Mammola and Isaia 2017; Hesselberg et al. 2019).

Orb spiders are often considered model organisms in the study of animal behaviour due to the ease with which quantitative measures of foraging behaviour can be obtained from photographs of the web, and due to their high behavioural flexibility (Zschokke and Herberstein 2005; Hesselberg 2015). Despite, mainly being found within the first 20 m of caves and not showing any troglomorphic adaptations, cave orb spiders in the genus *Meta* are one of the few cave organisms, where unique behavioural adaptations to subterranean life have been observed (Novak et al. 2010; Hesselberg et al. 2019). These include modified orb webs with missing frames and radii attaching directly to the substrate (Yoshida and Shinkai 1993; Simonsen and Hesselberg unpublished), possibly off-web foraging (Eckert and Moritz 1992; Smithers 2005a) and a life history which includes one or two instars spent outside of the subterranean environment (Smithers 2005b; Mammola and Isaia 2014).

Much less information is available on the other tetragnathid genera with troglophile members. *Okileucauge* and *Orsinome* are two small genera with currently 9 species all from China and Japan, and 16 species found mainly in Asia, respectively. We have almost no information on the ecology or behaviour of any of these species (World Spider Catalog 2019), although *Orsinome cavernicola* (Thorell, 1878) from Indonesia, an unidentified *Orsinome* from Tasmania and *Okileucauge geminuscavum* (Chen & Zhu, 2009) from China have been found in caves (Eberhard 1992; Chen and Zhu 2009). *Metellina* is a small genus currently containing 11 species with a cosmopolitan distribution (World Spider Catalog 2019), but it is in a state of flux with a considerable number of these 11 species added recently (Kallal and Hormiga 2018; Marusik and Larsen 2018). Not much is known on the ecology and behaviour of its members either, although some studies have

been conducted on mating and web-building behaviour in the common European species *M. segmentata* (Clerck, 1757) and *M. mengei* (Blackwall, 1870) (Prenter et al. 1994; Bridge et al. 2000; Tew and Hesselberg 2017, 2018). *Metellina* species are known to prefer dark and humid places to build their orb webs, although *M. mengei* can be found both in the dark interior, in clearings and at the edge of forests (Tew and Hesselberg 2017). At least two species, *M. merianae* (Scopoli, 1763) from Europe and the Middle East and *M. villiersi* (Denis, 1955) from Guinea are found in caves and classified as troglophiles (Hesselberg et al. 2019). While, no information is available on the biology of the latter, *M. merianae* have been the focus of a few studies. It is a relatively widespread species that is found in burrows, hollow trees and within the entrance and twilight zone of caves. Cave populations are known to co-exist with *Meta menardi* (Latreille, 1804) with limited spatial niche separation in that *M. merianae* are more likely to be found closer to the cave entrance, but with some temporal niche separation in that *M. merianae* show more pronounced difference in abundance throughout the year compared to *M. menardi* (Novak et al. 2010). Unlike, *Meta* orb spiders, *Metellina merianae* does not appear to show any behavioural adaptations to subterranean life as their orb webs resemble standard orb webs with frame threads and a large number of radii (Eckert and Moritz 1992; Novak et al. 2010), although this has not been systematically investigated. Here we aim to verify this claim by conducting a comparative study on overall size, relative leg length and detailed web geometry in the hypogean *M. merianae* and the epigean *M. mengei*.

Methods

Metellina merianae

Thirteen karst caves and abandoned mines with horizontal and easily accessible entrances were surveyed on Mallorca and Menorca, Balearic Islands, Spain during October and November 2018. Depending on the size, between 20 and 60 minutes were spent in the twilight zone visually searching for spider webs or lone spiders on cave floors, walls and ceilings. Out of the 13 caves (3 tiny, 4 small, 3 medium and 3 large), the following 5 harboured populations of *M. merianae*: Puig de Randa (large mine, UTM 31S 493175N, 4375097), Cova de Raviols (large cave, UTM 31S 458560, 4385672), Coves des Pillar (large cave, UTM 31S 464641, 4383561), Cova de Sa Trinxeta (medium cave, UTM 31S 464697, 4383578) and Cova de Sa Cometa des Morts (medium cave, UTM 31S 490691, 4408759). The size classifications used were: tiny (1–2 meters long and shed sized), small (2–5 meters long and room sized), medium (5–15 meters long) and large (longer than 15 meters).

Once the presence of *M. merianae* was confirmed, accessible webs built by juveniles or adult females within the twilight zone (here defined as 2–30 meters from the entrance) were measured with a ruler (to a precision of 0.1 cm) and the following data collected (which are standard measurements of field webs – see for example Hesselberg and Triana 2010): number of spirals above and below hub from which the average

number of spirals were calculated, the number of radii, horizontal and vertical diameter of the capture spiral, the diameter of the hub and free zone and the maximum distance from the web plane to either the cave wall or floor (depending on the orientation of the web). We used the ellipse-hub equation to calculate the area of the capture spiral (vertical diameter/2 * horizontal diameter/2 * π – (hub diameter/2)^2) (Herberstein and Tso 2000) as a measure of web area. We included web data from both juveniles and adult webs in order to obtain a decent sample size. This should not affect our comparisons with adult *M. mengei* webs (see below) since most characteristics of orb webs scale isometrically (Sensenig et al. 2011). The temperature at the site of the webs ranged from 11 °C to 14 °C and the humidity ranged from 72% to 93% rH.

The resident spider was collected in 90% ethanol and taken back to the laboratory, where the total length, the cephalothorax width, as a measure of spider size, and the combined patella-tibia length of leg I and III, as measurements of leg lengths, were measured with a digital calliper under a light microscope to a precision of 0.1 mm. The life stage of the spider was determined under the microscope as either juvenile (epigyne absent) or adult (epigyne present). In addition, distance from the cave entrance, temperature and humidity data was gathered at the location of the web as well as whether most of its attachment threads were connected to the floor, wall or ceiling. Finally, adult or subadult females without webs were collected directly from cave walls or occasionally from webs that were inaccessible for measurements in order to get additional spiders for the morphological measurements to ensure that only late instar juveniles and adult spiders were used.

Metellina mengei

Metellina mengei web and morphological data was collected in May and June 2018 from Wytham Woods, Oxfordshire, UK (UTM 30U 614887, 614887) as part of a larger comparative study of temperate tetragnathid spiders (Simonsen and Hesselberg, unpublished). 27 webs were surveyed within 2 m on either side of 10 randomly chosen 50 m transects. The temperature and the humidity in the vicinity of the webs ranged from 14 °C to 23 °C and from 55% to 86% rH. Only undamaged webs built by adult females were included in the survey and care was taken to sample webs from different height in the vegetation. The resident spiders were collected and brought to the laboratory, where they were killed in 70% ethanol before being measured. The same web characteristics and morphological data was gathered using similar methods as those described above for *M. merianae*.

Data analysis

To compare differences in overall morphology and web characteristics between the two species, we first performed a principal component analysis with the *prcomp()* function in R before using the *ggplot2* package (Wickham 2016) to generate ordination plots. To

control for differences in spider size, the following variables were used in linear mixed models (LMMs) as the response variable: relative patella-tibia length of leg I and III (patella tibia length divided by cephalothorax width), relative web area (web area divided by cephalothorax width squared), number of spiral turns per cm^2 web (average number of spiral turns divided by web area) and number of radii per cm^2 web (number of radii divided by web area) with species as predictor variable and location as a random effect. The LMMs were developed using the *lmer()* function from the *lme4* package (Bates et al. 2015). The two models were validated using diagnostic plots from the *mcp.fnc()* function from the *LMERConvenienceFunctions* package (Tremblay and Ransijn 2015). Relative web area and the number of capture spirals and radii per cm^2 web had to be log transformed to achieve normality. P values were found using the Type II Wald F-test.

In order to investigate the potential factors affecting the *M. merianae* webs, two LMMs were developed and validated as stated above with the number of radii and the area of the capture spiral as response variables, distance from the cave entrance, cephalothorax width, the location of the web (cave wall or floor), cave size (medium and large) and the number of radii (for the area of capture spiral model) as well as the interactions between cephalothorax width and the distance to the cave entrance and the location of the web as predictor variables and cave as a random effect. The models were reduced using the backwards elimination method based on P values using the Type II Wald F test. For all analyses, R (R Core Team 2018) was used with a significance level of 0.05. Figures were created with the *ggplot2* package (Wickham 2016).

Results

Comparisons of leg length and web characteristics between *Metellina merianae* and *M. mengei*

The differences in morphology and web parameters between *M. merianae* and *M. mengei* were visualised with a PCA ordination plots (Fig. 1), which showed that the two species differed substantially in size with the *M. merianae* about 1 ½ times larger than *M. mengei* (Fig. 1A; Table 1). The difference in web parameters were less pronounced and were almost entirely driven by differences in web area with *M. merianae* webs being more than twice as large as those of *M. mengei*, although they also showed much more variation in size (Fig. 1B; Table 1). Interestingly, despite their much larger webs, webs of *M. merianae* had slightly fewer spiral turns and radii than the webs of *M. mengei*.

However, to make meaningful comparisons between the hypogean *M. merianae* and the epigean *M. mengei*, we need to control for the difference in size (Table 1). The relative patella-tibia length (length divided by cephalothorax width) for leg I did not differ significantly between the two species (LMM: $F = 0.81$, $df = 1$, $P = 0.45$). However, *M. merianae* had a significantly longer relatively patella-tibia leg length for leg III than *M. mengei* (LMM: $F = 23.46$, $df = 1$, $P = 0.002$). The relative web area (here divided by cephalothorax width squared to keep it dimensionless) was not significantly

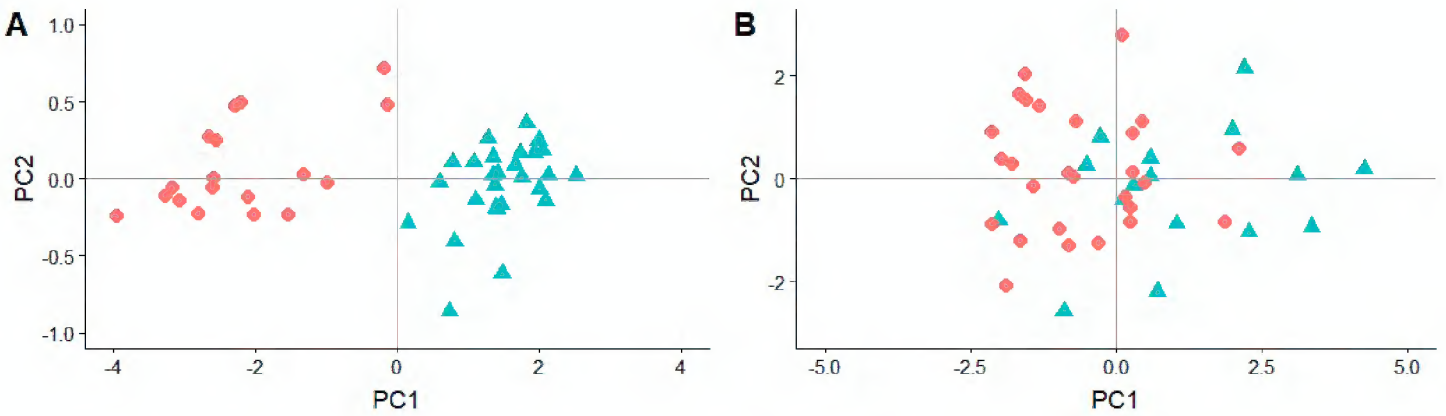

Figure 1. Principal component ordination plots of morphological and web parameters of *Metellina merianae* (red circle) and *Metellina mengei* (blue triangle). **A** Morphological variables (total length, cephalothorax width, patella-tibia length of leg I and leg III). The combined proportion of variance explained by PCA1 and PCA2 was 98%. **B** Web parameters (number of spirals, number of radii, vertical length of web, horizontal length of web and hub diameter). The combined proportion of variance explained by PCA1 and PCA2 was 78%.

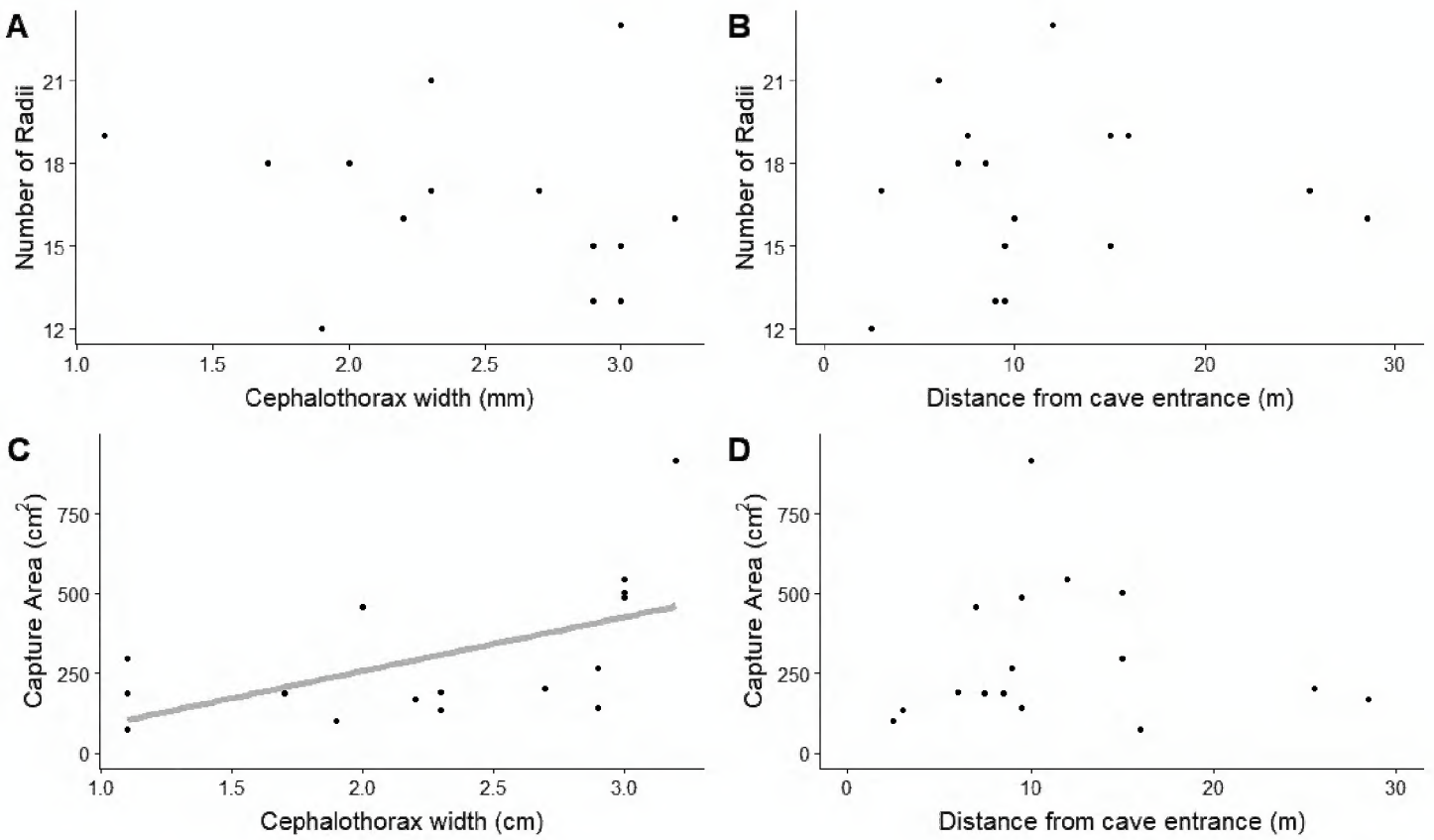

Figure 2. Area of webs of *Metellina merianae* in response to spider size and position in cave. **A** The number of radii in the web as a function of cephalothorax width of the resident spider. Not significant. **B** The number of radii in the web as a function of its distance from the cave entrance. Not significant. **C** The area of the capture spiral as a function of cephalothorax width. Significant. The grey line represents the equation ($y = 169x - 81$, $R^2 = 0.31$) arising from a simple linear regression. **D** The area of the capture spiral in the web as a function of its distance from the cave entrance. Not significant.

different between the two species (LMM: F = 0.41, df = 1, P = 0.54). However, both the number of spirals and the number of radii per cm^2 web area differed significantly with fewer in the webs of *M. merianae* (spiral number: LMM: F = 24.3, df = 1, P = 0.002; radii number: LMM: F = 20.7, df = 1, P = 0.004).

Table 1. Morphological traits and web characteristics of hypogean *Metellina merianae* spiders from caves in the Balearic Islands, Spain and epigean *Metellina mengei* from Wytham Woods, UK.

Variables	*Metellina merianae*	*Metellina mengei*
Morphological traits		
Sample size	18	27
Total length (mm)	7.1 ± 1.1	4.6 ± 0.5
Cephalothorax width (mm)	2.8 ± 0.5	1.6 ± 0.2
Patella-tibia length – leg I (mm)	5.8 ± 1.1	3.1 ± 0.3
Relative patella-tibia length – leg I[a]	2.05 ± 0.25	1.99 ± 0.14
Patella-tibia length – leg III (mm)	2.8 ± 0.6	1.3 ± 0.1
Relative patella-tibia length – leg III[a]	0.98 ± 0.13	0.81 ± 0.08
Web characteristics		
Sample size	16	27
Web area (cm^2)	96.7 ± 71.0	36.5 ± 15.7
Relative web area[b]	2113 ± 1992	1513 ± 652
Average number of spiral turns	13.0 ± 3.0	15.8 ± 4.1
Spiral turns per cm^2 web area	0.21 ± 0.14	0.52 ± 0.26
Number of radii	16.9 ± 3.0	18.5 ± 3.0
Radii per cm^2 web area	0.27 ± 0.18	0.62 ± 0.30

Mean ± Std. dev.; [a] Relative length is original length divided by cephalothorax width; [b] Relative web area is original web area divided by cephalothorax width squared

Factors affecting web characteristics in the hypogean *Metellina merianae*

Webs from 11 juvenile and 5 adult *M. merianae* were used in the analysis. The number of radii in the webs was not significantly influenced by the distance from the cave entrance (LMM: F = 0.41, df = 1, P = 0.53), whether webs were found on the wall or the floor of the cave (LMM: F = 0.001, df = 1, P = 0.98), the size of the cave (LMM: F = 3.26, df = 2, P = 0.45) or the size of the spider (LMM: F = 0.43, df = 1, P = 0.53) nor were any of the interactions tested found to be significant (data not shown). Similarly, the size of the web did not depend on the distance from the cave entrance (LMM: F = 0.001, df = 1, P = 0.98), whether webs were found on the wall or the floor of the cave (LMM: F = 1.68, df = 1, P = 0.26), the number of radii (LMM: F = 0.17, df = 1, P = 0.68), the size of the cave (LMM: F = 0.70, df = 2, P = 0.81) or any of the interactions tested (data not shown). However, the size of the capture area was positively related to the cephalothorax width of the resident spider (LMM: F = 5.39, df = 1, P = 0.04).

Discussion

The most obvious convergent adaptations to a subterranean life-style are the morphological adaptations including limb elongation, depigmentation and lack or reduction of eyes (Poulson and White 1969; Christensen 2004; Culver and Pipan 2009). Our results confirm the findings of previous studies (Eckert and Moritz 1992; Novak et al. 2010) that *Metellina merianae* do not show any clear morphological adaptations. Similarly, our results confirm that *M. merianae* build large, normal looking orb webs enclosed by a complete set of frame threads, and therefore do not show the clear behavioural adaptations reported in the sister genus *Meta* (Mammola and Isaia 2014; Hesselberg et al.

2019). However, our results indicate some differences in both morphological and web characteristics between *M. merianae* and its epigean sister species *M. mengei*.

In terms of morphology, *M. merianae* were about 50% longer and had a 75% wider cephalothorax than *M. mengei*. There is some indication that Foster's rule for larger size for small animals on islands, may also hold for cave animals (Whittaker 1998; Trontejl et al. 2012), although see Mammola (2018) for a cautionary note on the cave-as-islands paradigm. For example, troglomorphic cave millipedes are significantly longer than epigean species (Liu et al. 2017). However, *M. merianae* are less than half the size of the cave orb spiders in the genus *Meta* (Hesselberg et al. 2019). We furthermore found no difference in the relative length of the front legs between *M. merianae* and *M. mengei*, although the relative length of leg III was 20% longer in *M. merianae*. The first pair of legs in orb spiders is important during prey attack behaviour and for measuring distances during construction of the capture spiral (Robinson et al. 1969; Vollrath 1987), while leg III seemingly plays a much less significant role and is mainly used to grip the radii during capture spiral construction (Eberhard and Hesselberg 2012).

In terms of foraging behaviour, or web geometry, the webs of cave populations of *M. merianae* were superficially similar to those of the woodland *M. mengei* in that they both had a similar number of radii and spiral turns, although the area enclosed by the capture spiral was two and a half times larger in *M. merianae*. When controlling for the difference in spider size, the webs between the two species did not differ significantly in size. Interestingly, when controlling for web area, webs of *M. merianae* were larger spaced (fewer spiral turns) and had fewer radii than *M. mengei*. Thus, while *M. merianae* webs differed substantially from webs of the cave spider *Meta menardi* in that they were larger and had intact frame threads, they had relatively few radii and radii spiral turns similar to the webs of *Meta menardi* (Simonsen and Hesselberg unpublished). These modifications could be viewed as adaptations to the cave environment. The number of radii is an important determinant of prey stopping potential (Sensenig et al. 2012), suggesting that these webs are not adapted to capture heavy or fast flying prey. The larger distances between capture spiral turns, however, suggest that these webs are optimised to capture large, but weak prey (Sandoval 1994; Blackledge and Zevenbergen 2006). Both of these observations fit with the prey likely to be encountered in caves, where the majority of flying insects are relatively spindly and slow-flying gnats, moths and caddisflies (Smithers 2005a; Novak et al. 2010).

In this preliminary study on the drivers of web characteristics in *M. merianae* from caves, the size of the cave was not an important determinant. However, it is worth noting that *M. merianae* were only found in medium and large caves. They were not found in any of the 7 tiny and small caves visited as part of this study, possibly because the aggressive web-invading cellar spider *Pholcus phalangoides* (Füssli, 1775) were relatively abundant in the majority of these smaller caves (Jackson and Brassington 1987). Interestingly, the current study did not find any effect on the web characteristic of the distance from the cave entrance or whether webs were on the wall or floor, although it

is worth noting that the sample size in the current study was limited. Not surprisingly, we found that spider size positively influenced web area. Previous studies (Eckert and Moritz 1992; Novak et al. 2010) did not look at the structure of the web, but only recorded presence/absence. Eckert and Moritz (1992) report that *M. merianae* populations in Germany prefer cold and damp caves, although in the current study they were also found in relatively dry (down to 73% rH) and warm (up to 14 °C) caves on the Balearic Islands. Similar tolerance to high temperatures and drier caves were also found in a Slovenian population (Novak et al. 2010). It is possibly that preferences differ in different geographical locations, although clearly much more data is needed on how cave characteristics affect both the presence and the webs of *M. merianae*.

Conclusions

In conclusion, the present study finds evidence of some minor morphological differences between hypogean and epigean *Metellina* with the possibility that the larger size of *M. merianae* could be an adaptation to subterranean life. Similarly, minor differences in web geometry were evident with *M. merianae* webs having larger distances between spiral turns and fewer radii relative to web area than those of the epigean *M. mengei*. However, the present study is not able to determine if these differences are potential indications of a transition process towards adaptation to subterranean life or are instead the results of behavioural flexibility. Orb spiders are well known for displaying a significant degree of behavioural flexibility in the structure of their orb webs in response to a range of biotic and abiotic variables (Heiling and Herberstein 2000; Hesselberg 2015; Eberhard in press). The araneid *Araneus diadematus* (Clerck, 1758), for example, slightly reduces the number of radii and significantly increased the distance between capture spiral turns when going from building webs at 24 °C to 12 °C in a laboratory study (Vollrath et al. 1997). A similar mechanism could explain the differences we found between webs built in the colder caves compared to the warmer woodland. Humidity is also known to affect web geometry (Vollrath et al. 1997), and higher humidity such as found in caves could render capture threads more efficient at retaining prey (Boutry and Blackledge 2013), thus potentially requiring less capture silk as found in our study. Wind, although not measured in our study, also affects orb geometry. However, caves are likely to experience less windy conditions than in woodland, which should, in contrast to our findings, result in webs with more radii and capture spiral turns (Vollrath et al. 1997; Wu et al. 2013). Clearly more studies are needed under controlled laboratory conditions and on the web geometry of *M. merianae* from different cave and epigean environments, taking advantage of the fact that this species can also be found in dark and damp woodland, in order to investigate the intriguing possibility that this species is in the process of evolving behavioural adaptations to the hypogean environment mirroring the likely process that has taken place in the larger sister genus *Meta*.

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